

8

Food Consumption and Feeding Habits

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8.1 Introduction

Although it is widely recognized that sharks and other elasmobranchs often play a role in the transfer of energy between upper trophic levels within marine ecosystems, our understanding of the dynamics of prey consumption and processing of food in elasmobranchs remains rudimentary. To fully comprehend energy flow through elasmobranchs in marine communities it is necessary not only to know what they eat, but also to characterize the rates at which they ingest, digest, and process energy and nutrients contained in prey that is consumed. As with other areas of elasmobranch biology, investigations on dynamics of feeding and processing food lag behind such studies on other marine fishes and vertebrates. By far the most common elasmobranch feeding studies simply describe stomach contents of a particular species in a particular location. Rate of consumption, feeding patterns, and the fate of food once ingested have been examined for very few species of elasmobranchs.

The spiral valve-type intestine present in elasmobranchs has been referred to as a primitive design and there has been speculation that food is processed differently as it passes through the digestive systems of elasmobranchs than for most teleost fishes. The different digestive morphology present in elasmobranchs might be expected to influence time for passage of food through the alimentary canal, the efficiency of energy and nutrient absorption, the rate of consumption, and ultimately the amount of energy available for growth and other needs.

In this chapter we review information on patterns of food consumption and processing of food in the digestive tracts of elasmobranchs, with special emphasis on sharks. In general terms we examine food consumption from several perspectives: what is eaten, feeding patterns, and how much is eaten. Our discussion includes dietary overlap and dietary breadth among species of elasmobranchs as well as presumptions that have been made about food partitioning in these species. Second, we review the current state of knowledge concerning processing of food once ingested by elasmobranchs, including rates of digestion and evacuation of food from the stomachs and entire intestinal tracts of elasmobranchs. Absorption, assimilation, and conversion of ingested food into new tissue are also discussed. For most topics, we include methodological considerations relevant for experimental design and interpretation of results for past or future elasmobranch feeding studies. We conclude by offering some recommendations for future work.

8.2 Diet

The feeding biology of elasmobranchs has been investigated to understand the natural history of a particular species, the role of elasmobranchs in marine ecosystems, the impact of elasmobranch predation on economically valuable or endangered prey, and various other reasons. For these reasons researchers have attempted to describe the diets of elasmobranchs, ranging from the stomach contents of a single shark, to detailed examination of the quantity of each prey item, feeding periodicity, and frequency.

8.2.1 Quantification of Diet

Many early descriptions of the diets of different elasmobranch species were simply lists of prey items recovered from their stomachs (Coles, 1919; Breder, 1921; Gudger, 1949; Clark and von Schmidt, 1965; Randall, 1967; Dahlberg and Heard, 1969). Other studies have quantified prey types found in stomachs using counts: the number of stomachs with a specific prey (frequency of occurrence; O), the total number of a specific prey found in stomachs (N); or using total weight (W) or volume (V) of a specific prey item (Stevens, 1973; Matallanas, 1982; Stillwell and Kohler, 1982; Snelson et al., 1984; to cite a few). Each of these terms has shortcomings for accurately expressing the amount of various prey that constitute the diet of a consumer (Bowen, 1996; Mumtaz Tirasin and Jorgensen, 1999; Liao et al., 2001). For example, expression of stomach contents with counts may give the impression that a specific prey item that occurs very frequently in stomachs represents one of the most important prey items. However, if these prey are small, they may represent only a small proportion of the total food consumed. Similarly, if diet is expressed in terms of weight or volume, consumption of a single large prey item would imply that this prey is a major component of the diet, when in fact very few individuals may have consumed it. To overcome such limitations, diet has often been reported in terms of a combination of several indices, such as the index of relative importance (Cortés, 1997, 1999):

$$(IRI) = \%F(\%W + \%N) \quad (8.1)$$

Compound expressions of diet provide less biased estimates of the contribution of various prey in the diet of a consumer, but their use remains controversial (Cortés, 1998; Hansson, 1998). Nonetheless Cortés (1997) suggested that presentation of stomach contents of sharks in terms of %IRI would both provide estimates of the diet that were intuitive and that would allow more direct comparison among studies.

Reliance on stomach contents to quantify diet of an animal also has limits. For example, rate of digestion of prey items in the stomach may vary with size and type of prey, and therefore items that are digested slowly may be overrepresented in stomachs examined. Capture technique may also influence contents in stomachs. Stomach contents of sharks captured at depth may be regurgitated, or differentially regurgitated, as the sharks are brought to the surface. Similar presumptions have been made in a number of studies where sharks were captured using gillnets.

Ecological energetics are a common framework for consideration of the fate of food consumed by animals, relating consumption to life activities through a common unit of measure, the calorie or joule (Kleiber, 1975; Brafield and Llewellyn, 1982). Diet in energetic terms would refer to the amount of

energy that each item ingested contributes toward the total amount of energy consumed by an animal. The first law of thermodynamics (conservation of energy) necessitates that all energy consumed by an animal be balanced by energy used (for growth, metabolism, or reproduction) and energy lost (in feces and urine) (Kleiber, 1975). Therefore, quantification of diet in energetic terms (the amount of energy contributed by each prey type) might provide a method for expressing diet in standardized and biologically meaningful terms. Difficulties of such an approach include determination of initial size of each prey item consumed and energy content of each prey type (Scharf et al., 1998). An additional consideration far beyond simply quantifying stomach contents would be the inclusion of the energetic costs of capturing various types of prey. Although such analyses would be extremely challenging given current technology available, a general understanding of the amount of energy expenditure required to capture specific prey would provide insight into net energy gains resulting from capture and consumption of particular prey types.

8.2.2 Broad Dietary Groups

As carnivores, elasmobranchs consume a limited array of prey in comparison to teleosts, which also include omnivores and herbivores. However, there is a wide range of prey consumed by elasmobranchs, ranging from very small plankton to whales. Plankton or small crustaceans are consumed by large, filter-feeding elasmobranch species, including manta rays (*Manta birostris*) and basking (*Cetorhinus maximus*), whale (*Rhincodon typus*), and megamouth sharks (*Megachasma pelagios*) (Gudger, 1941; Hallacher, 1977; Compagno, 1990; Sims and Merrett, 1997; Sims and Quayle, 1998). The diet of most species of sharks includes teleosts, and for many species the percentage of stomachs containing teleosts exceeds 90%, particularly for sharks in the genus *Carcharhinus* (Bass et al., 1973; Stevens and Wiley, 1986; Stevens and McLoughlin, 1991; Cliff and Dudley, 1992; Salini et al., 1992; Castro, 1993; Dudley and Cliff, 1993), closely related sharpnose (*Rhizoprionodon*) and hammerhead (*Sphyrna*) species (Stevens and Lyle, 1989; Stevens and McLoughlin, 1991; Simpfendorfer and Milward, 1993) as well as mackerel sharks (Lamnidae) (Stillwell and Kohler, 1982; Gauld, 1989). Elasmobranchs are common prey of many sharks and may form a large portion of the diet of some large carcharhinids (Cliff and Dudley, 1991a; Dudley and Cliff, 1993; Wetherbee et al., 1996; Gelsleichter et al., 1999), hammerheads (Stevens and Lyle, 1989; Cliff, 1995), sixgill (*Hexanchus griseus*) and sevengill (*Notorynchus cepedianus*) sharks (Ebert, 1991, 1994) and white (*Carcharodon carcharias*) and tiger (*Galeocerdo cuvier*) sharks (Gudger, 1932; Cliff et al., 1989; Lowe et al., 1996).

Cephalopods are also common prey items. Many pelagic sharks feed on squid (Backus et al., 1956; Stillwell and Casey, 1976; Kohler, 1987; Smale, 1991), and demersal sharks often feed on octopus (Relini Orsi and Wurtz, 1977; Mauchline and Gordon, 1983; Baba et al., 1987; Castro et al., 1988; Kubota et al., 1991; Stevens and McLoughlin, 1991; Carrassón et al., 1992; Ebert et al., 1992; Ebert, 1994; Waller and Baranes, 1994). Small, benthic catsharks (Scyliorhinidae), smoothhounds (Triakidae), and hornsharks (Heterodontidae) frequently prey upon mollusks (Talent, 1976; Lyle, 1983; Menni, 1985; Segura-Zarzosa et al., 1997; Gelsleichter et al., 1999), and crustaceans form a large portion of the diet of a number of bottom-feeding carcharhinid species (Medved et al., 1985; Lyle, 1987; Stevens and McLoughlin, 1991; Salini et al., 1992; 1994; Simpfendorfer and Milward, 1993), hammerheads (Castro, 1989; Cortés et al., 1996; Bush, 2002), sharpnose (Gómez Fermin and Bashirulah, 1984; Devadoss, 1989; Gelsleichter et al., 1999), smoothhounds (Talent, 1982; Taniuchi et al., 1983; King and Clark, 1984; Vianna and Amorim, 1995; Rountree and Able, 1996; Smale and Compagno, 1997), catsharks (Ford, 1921; Macpherson, 1980; Lyle, 1983; Cross, 1988; Ebert et al., 1996; Heupel and Bennett, 1998), and batoids (Ajayi, 1982; Smith and Merriner, 1985; Ebert et al., 1991; Smale and Cowley, 1992; Barry et al., 1996; Ellis et al., 1996; Schwartz, 1996).

Large sharks occasionally consume vertebrates other than fish. Birds have been found in the stomach of bull sharks (*Carcharhinus leucas*; Tuma, 1976) and tiger sharks (Saunders and Clark, 1962; Dodrill and Gilmore, 1978; Heithaus, 2001a; Carlson et al., 2002) and may compose a large part of the diet of tiger (Bass et al., 1973; Stevens, 1984; Simpfendorfer, 1992; Lowe et al., 1996) and white sharks (Randall et al., 1988). Reptiles (turtles and snakes) are occasionally eaten by carcharhinid sharks (Heatwole et al., 1974; Tuma, 1976; Lyle, 1987; Lyle and Timms, 1987; Cliff and Dudley, 1991a) and white sharks

(Long, 1996; Fergusson et al., 2000) and are common in the stomachs of tiger sharks (Witzell, 1987; Stevens and McLaughlin, 1991; Simpfendorfer, 1992; Lowe et al., 1996; Heithaus, 2001a). Marine mammals are frequently preyed upon by large sharks such as white and tiger sharks (Bell and Nichols, 1921; LeBoeuf et al., 1982; Stevens, 1984; Corkeron et al., 1987; Cliff et al., 1989; Lowe et al., 1996; Dudley et al., 2000; Heithaus, 2001a) and have been found in stomachs of carcharhinid sharks (Bass et al., 1973; Cliff and Dudley, 1991a; Wetherbee et al., 1996) and of sleeper sharks (*Somniosus*) (Scofield, 1920), sixgill and sevengill sharks (Hexanchidae) (Ebert, 1991, 1994). The unusual tooth and jaw morphology of cookie-cutter sharks (*Isistius brasiliensis* and presumably *I. plutodon*) enables these sharks to maintain an essentially parasitic lifestyle by removing plugs of flesh from large vertebrates (tunas, billfish, dolphins, and whales) and from squid (Strasburg, 1963; Jones, 1971; Jahn and Haedrich, 1988; Muñoz-Chapuli et al., 1988; Shirai and Nakaya, 1992). Readers are referred to Cortés (1999) for a summary of standardized diet compositions of 149 shark species.

8.2.3 Diet Shifts

Adequate representation of the diet of a species of elasmobranch is complicated by differences in diet that occur within species among individuals of different sizes, geographical locations, and during different seasons. Ontogenetic change in feeding habits is an almost universal phenomenon in fishes and thus its occurrence in elasmobranchs is not surprising considering that, as many species of sharks and rays increase in size, there also are changes in habitat occupied, movement patterns, swimming speed, size of jaws, teeth and stomachs, energy requirements, experience with prey, vulnerability to predation, and other factors that result in variable exposure to prey or improved ability of larger sharks to capture different prey items (Graeber, 1974; Weihs et al., 1981; Stillwell and Kohler, 1982; Lowe et al., 1996).

Although diet shifts are more often reported qualitatively rather than based on rigorous statistical analysis, there are many reports of a shift from a diet of invertebrates to a diet that is more varied or that includes more teleosts (Olsen, 1954; Capapé, 1974, 1975; Capapé and Zaouali, 1976; Talent, 1976; Jones and Geen, 1977; Mauchline and Gordon, 1983; Smale and Cowley, 1992; Stillwell and Kohler, 1993; García de la Rosa and Sánchez, 1997; Platell et al., 1998; Smale and Goosen, 1999; Kao, 2000; Jakobsdóttir, 2001). There are also multiple studies that document increased consumption of elasmobranchs (Matallanas, 1982; Cortés and Gruber, 1990; Cliff and Dudley, 1991a; Smale, 1991; Lowe et al., 1996; Simpfendorfer et al., 2001a,b) and marine mammals (Tricas and McCosker, 1984; Ebert, 1994) with increasing size of shark. A number of studies, however, found no ontogenetic dietary changes (Kohler, 1987; Cliff and Dudley, 1991b; Matallanas et al., 1993; Clarke et al., 1996; Cortés et al., 1996; Segura-Zarzosa et al., 1997; Avsar, 2001; Jakobsdóttir, 2001).

There are also examples of geographical differences in the diets of several wide-ranging species of sharks. For example, the diets of spiny dogfish (*Squalus acanthias*), blue (*Prionace glauca*), sandbar (*Carcharhinus plumbeus*), blacktip (*C. limbatus*), and bull sharks all differed among locations in the Atlantic, Pacific, and Indian Oceans (Gudger, 1948, 1949; Holden, 1966; Rae, 1967; Wass, 1971; Stevens, 1973; Gubanov and Grigor'yev, 1975; Tuma, 1976; Jones and Geen, 1977; Tricas, 1979; Kondyurin and Myagkov, 1982; Stevens et al., 1982; Sarangdhar, 1983; Snelson et al., 1984; Medved, 1985; Cliff et al., 1988; Harvey, 1989; Cliff and Dudley, 1991a; Dudley and Cliff, 1993; Lowe et al., 1996). Variation of diet among locations is exemplified by the tiger shark, which has a diet that differed substantially among areas sampled worldwide (DeCrosta et al., 1984; Simpfendorfer, 1992; Lowe et al., 1996; Simpfendorfer et al., 2001a). Diet may differ within a species even between locations that are relatively close, as has been found for sandbar (Lawler, 1976; Medved et al., 1985; Stillwell and Kohler, 1993) and lemon sharks (*Negaprion brevirostris*; Springer, 1950; Schmidt, 1986; Cortés and Gruber, 1990), and the star-spotted smoothhound (*Mustelus manazo*; Yamaguchi and Taniuchi, 2000). Habitat type and water depth have also been found to influence diet composition (Stillwell and Kohler, 1982, 1993; Kohler, 1987; Cortés et al., 1996; Smale and Compagno, 1997; Webber and Cech, 1998). Several authors have reported differences in the diet between sexes of sharks (Bonham, 1954; Matallanas, 1982; Hanchet, 1991; Stilwell and Kohler, 1993; Simpfendorfer et al., 2001a), which may be due to sexual segregation within species and different sizes attained by males and females. In all, findings of geographical differences in diet of sharks are not surprising considering the diversity of prey in different regions and

the apparent plasticity of feeding behaviors among sharks (see Heithaus, Chapter 17 of this volume, for a more complete discussion).

Variation in feeding of sharks is further demonstrated by seasonal differences in diet that have been reported within species (Capapé, 1974; Talent, 1976; Jones and Geen, 1977; Tricas, 1979; Lyle, 1983; Olsen, 1984; Kohler, 1987; Dudley and Cliff, 1993; Waller and Baranes, 1994; Cortés et al., 1996; Nagasawa, 1998; Platell et al., 1998; Allen and Cliff, 2000; Horie and Tanaka, 2000). Seasonal differences in diet presumably reflect seasonal migration of sharks or of their prey. For example, Matallanas (1982) reported seasonal shifts in the most important teleosts in the diet of kitefin sharks (*Dalatias licha*) and Stillwell and Kohler (1982) described seasonal shifts between consumption of fish and cephalopods by the mako shark (*Isurus oxyrinchus*). There is also evidence of a diet shift in leopard sharks (*Triakis semifasciata*) sampled at a single location during two periods 25 years apart, which may be indicative of community changes (Kao, 2000).

8.2.4 Feeding Relationships

There have been relatively few investigations comparing diets of sympatric species of elasmobranchs. In several studies, standard ecological indices of similarity were used to calculate dietary overlap among elasmobranch species, among elasmobranchs and teleosts caught in the same location, or among different size classes of a single species. Such comparisons represent initial attempts to characterize food partitioning and competition among elasmobranchs and co-occurring teleosts. Ecological indices of dietary breadth or diversity have also been calculated for several species of elasmobranchs to examine the degree of feeding specialization.

The available evidence indicates that both food partitioning and competition for food resources are likely to occur in marine communities where elasmobranchs occur. Dietary overlap among sympatric species of elasmobranchs has been characterized — qualitatively or using quantitative indices — as low (Macpherson, 1981; Baba et al., 1987; Carrassón et al., 1992; Orlov, 1998), moderate (Relini Orsi and Wurtz, 1977; Smale and Compagno, 1997; Orlov, 1998) to substantial (Macpherson, 1980; Ellis et al., 1996), high (Salini et al., 1990; Platell et al., 1998), and variable depending on the species compared (Macpherson, 1981; Euzen, 1987). Varying degrees of diet overlap have also been described for co-occurring elasmobranchs and teleosts (Blaber and Bulman, 1987; Ali et al., 1993; Clarke et al., 1996), or for elasmobranchs and marine mammals (Clarke et al., 1996; Heithaus, 2001b). At the intraspecific or intrapopulation level, increased dietary overlap is most often encountered between pairs of consecutive size classes (Cortés et al., 1996; Wetherbee et al., 1996, 1997; García de la Rosa and Sánchez, 1997; Platell et al., 1998; Kao, 2000; Simpfendorfer et al., 2001a; Koen Alonso et al., 2002), or between similar size classes of elasmobranchs and teleosts (Platell et al., 1998). Food overlap also tends to be high between adjacent geographic locations (Yamaguchi and Taniuchi, 2000; Simpfendorfer et al., 2001a).

Diets of elasmobranchs vary from highly specialized to very generalized. Specialized diets include those of elasmobranchs that consume zooplankton, crustaceans, and cephalopods as discussed in an earlier section. In contrast, a number of top predators, such as bull and tiger sharks, have very generalized diets. Varying degrees of specialization have been reported in studies that calculated true measures of diversity (Macpherson, 1981; Blaber and Bulman, 1987; Clark et al., 1989; Carrassón et al., 1992; Ali et al., 1993; Cortés et al., 1996; Ellis et al., 1996; Simpfendorfer et al., 2001a) or that reported only the total number of different prey types or contained qualitative statements about dietary diversity (Chatwin and Forrester, 1953; Capapé and Zaouali, 1976; Segura-Zarzosa et al., 1997; Smale and Compagno, 1997; Gelsleichter et al., 1999). Dietary breadth tends to increase with size or age in some cases (Talent, 1976; Cortés and Gruber, 1990; Lowe et al., 1996; Wetherbee et al., 1996, 1997) and decrease in others (Smale and Compagno, 1997; Platell et al., 1998; Yamaguchi and Taniuchi, 2000; Simpfendorfer et al., 2001a).

Because of the widespread occurrence of ontogenetic, geographical, and seasonal changes in feeding habits discussed above, very few studies on the diet of sharks have been extensive enough to provide a comprehensive description of the diet for a species. Additionally, the diversity of prey found in stomachs generally increases with the number of stomachs sampled. The issue of sample sufficiency can be addressed by using cumulative prey curves to determine whether a sufficient number of stomachs have been examined to describe precisely the diet of the species in question (see Ferry and Cailliet, 1996;

Cortés, 1997, and references therein). Clearly, there is ample opportunity for improving our understanding of aspects of the feeding ecology of elasmobranchs at the organism, population, community, and ecosystem level through additional and more focused research.

8.2.5 Feeding Patterns

Understanding a consumer's feeding patterns requires more than knowledge of the prey items that make up its diet. The dynamics of the feeding process must be accounted for, and thus to understand the ecological interaction between predator and prey we must have knowledge of the amount of food ingested and the feeding frequency of the predator. Analysis of stomach contents allows inference of feeding patterns through reconstruction of meal sizes, ingestion times, feeding duration, and feeding frequency. The frequency of occurrence of empty stomachs, the number, weight, and stage of digestion of food items, in combination with knowledge on the gastric evacuation dynamics of each food item, all give insight into the feeding pattern of a predator.

The occurrence of high proportions of empty stomachs in shark diet studies and in commercial fisheries operations is common (Wetherbee et al., 1990). Use of longlines to capture sharks may attract more animals with empty stomachs, but this is unlikely when using passive gear such as gillnets or active gear such as trawls. Frequent occurrence of empty stomachs, combined with the observation that there are often few food items — many of them in advanced stages of digestion — in shark stomachs — e.g., in the juvenile sandbar shark (Medved et al., 1985) and the juvenile lemon shark (Cortés and Gruber, 1990) — lends support to the notion that many sharks are intermittent rather than continuous feeders, because otherwise one would expect to regularly find multiple food items at different stages of digestion and few empty stomachs. Demersal carnivores that feed on invertebrate prey, such as many skates and rays (Bradley, 1996), and filter feeding zooplanktivorous sharks are obvious exceptions to this pattern (Baduini, 1995; Sims and Quayle, 1998), as they feed more continuously.

Feeding frequency can be estimated from the total time required to complete gastric evacuation and the proportion of empty stomachs in a sample (Diana, 1979). Based on this method, Jones and Geen (1977) estimated that mature spiny dogfish would feed only every 10 to 16 days after completely filling their stomachs, whereas Medved et al. (1985) and Cortés and Gruber (1990) estimated a feeding frequency of 95 h and 33 to 47 h for juvenile sandbar and lemon sharks, respectively.

Gastric evacuation experiments (Section 8.3.2) allow development of qualitative scales describing the various stages of digestion of food items. These qualitative scales can then be used to calculate the difference between the least and most advanced stages of digestion of food items found in stomachs of field-sampled animals, and infer feeding duration. Medved et al. (1985), Cortés and Gruber (1990), and Bush and Holland (2002) used this approach to obtain estimates of feeding duration for juvenile sandbar (7 to 9 h), lemon (11 h), and scalloped hammerhead sharks (*Sphyrna lewini*; 9 to 10 h). The occurrence of food items in different stages of digestion in stomachs of juvenile lemon and sandbar sharks caught at the same time also indicated that feeding in these two species was asynchronous; i.e., there was no preferred feeding time for all individuals of a population, a pattern believed to be prevalent in most shark species. Conversely, Kao (2000) reported some evidence for feeding synchronicity in the leopard shark off the central California coast. Results from Medved et al. (1985) and Cortés and Gruber (1990) for juvenile sandbar and lemon sharks, respectively, did not reveal increased food consumption at night or during a particular tidal phase. However, these studies did not estimate meal ingestion times, as we explain in the next paragraph.

Cortés (1997) reviewed the numerous methodological issues that can affect the interpretation of diel feeding chronology in fishes and elasmobranchs. In addition to the effect of passive vs. active sampling gear, experimental design, and statistical analysis of results, he cautioned against using the weight of stomach contents alone to assess diel feeding (dis)continuity and to interpret diel feeding chronology. To estimate preferred feeding times it is also necessary to reconstruct meal ingestion times using qualitative stage-of-digestion scales. In captivity, Longval et al. (1982) found a cyclical feeding pattern in juvenile lemon sharks, with peak consumption followed by several days of reduced food intake. The evidence for sharks, as exemplified by work on juvenile lemon sharks, supports the concept of a cyclical pattern of feeding motivation observed in many vertebrates, whereby relatively short feeding bouts would

be followed by longer periods of reduced predatory activity until the return of appetite, which in the lesser spotted dogfish (*Scyliorhinus canicula*) was found to be inversely correlated with gastric evacuation rate (Sims et al., 1996).

8.2.6 Trophic Levels

It is commonly accepted that sharks are top predators in many marine communities. However, until recently, virtually no quantitative estimates of trophic levels existed for sharks. Cortés (1999) calculated standardized diet compositions and estimated trophic levels for 149 shark species belonging to 23 families using published trophic levels of prey categories, largely based on the Ecopath II model (Christensen and Pauly, 1992). He concluded that sharks as a group are tertiary consumers (trophic level > 4) that occupy trophic positions similar to those of marine mammals and higher than those of seabirds. Measurement of stable isotopes of nitrogen and carbon in tissues of marine consumers is an alternative approach to estimating trophic level based on stomach contents. To date, only two studies on sharks have used stable isotope analysis to estimate trophic level; in the basking shark (Ostrom et al., 1993) and Greenland shark (*Somniosus microcephalus*; Fisk et al., 2002). Fisk et al. (2002) also used concentrations of organochlorine contaminants to estimate the trophic level of Greenland sharks, concluding that results from stable isotope analysis and this technique did not agree. They attributed the lower trophic level obtained through stable isotope ($\delta^{15}\text{N}$) analysis compared to that from contaminant analysis to urea retention in elasmobranch tissues for osmoregulation, which could result in lower levels of $\delta^{15}\text{N}$ and thus underestimate trophic level. Further investigation of the effect of urea retention on $\delta^{15}\text{N}$ levels is thus required (Fisk et al., 2002) along with comparisons of stable isotope and dietary-based estimation of trophic levels.

8.3 Food Consumption

Feeding ecology is an important aspect of the life-history strategy of a species that can be adequately expressed through determination of food consumption rates. Daily rates of food consumption are in turn dependent on gastric evacuation rates. Measurement of daily rates of food consumption and digestion rates require regular collection of stomach contents of fish caught in the wild and fish held in captivity in the laboratory or field. This poses a particularly difficult problem for those studying elasmobranchs and sharks in particular, because of the difficulty of keeping them in captivity and the logistical requirements of extended field sampling. Additionally, rates of consumption in teleost fishes may vary depending upon a myriad of intrinsic (e.g., age, feeding history, reproductive status) and extrinsic factors (e.g., geographical location, habitat type, water temperature, prey availability). The scarcity of information on food consumption rates of elasmobranchs is thus hardly surprising.

8.3.1 Daily Ration

Daily ration is the mean amount of food consumed on a daily basis by individuals of a population, generally expressed as a proportion of mean body weight. Although an individual does not ingest the same amount of food everyday and may not even feed daily, daily ration is a good measure for comparative studies (Wetherbee et al., 1990). There are two basic approaches for estimating daily ration: (1) *in situ* (field-derived) methods, which require knowledge of the amount of food found in stomachs of fish sampled in the wild and of the gastric evacuation dynamics of the ingested foodstuffs, and (2) bioenergetic models, which estimate food consumption based on the other components of the bioenergetic equation (growth, metabolism, excretion, and egestion).

With field-based methods, daily ration cannot be estimated by simply examining stomach contents because the amount of food found in stomachs is a function of both ingestion and digestion rates (Wetherbee et al., 1990). Cortés (1997) reported that there has been very little investigation of the applicability to elasmobranchs of the most common models used to estimate daily ration in teleosts. *In situ* methods of estimation that have been used for elasmobranchs include those by Elliott and Persson

(1978), Diana (1979), Eggers (1979), Pennington (1985), and Olson and Mullen (1986). Cortés (1997) concluded that the Diana and Olson-Mullen methods applied better to intermittent feeders, such as most sharks, and that these models were also based on less restrictive assumptions and required comparatively less demanding sampling regimens. Given the absence of error analyses of the estimates of daily ration in elasmobranch studies, Cortés (1997) advocated the use of resampling techniques, such as bootstrapping, or Monte Carlo simulation to enable statistical testing of differences between estimates obtained through different models and generally to provide a picture of the variability associated with those point estimates.

Laboratory approaches to estimating daily ration are based on a bioenergetic or energy budget equation (Winberg, 1960), which relates consumption (C) to growth (G), metabolism (M), excretion (urine, U), and egestion (feces, F):

$$C = G + M + U + F \quad (8.2)$$

The daily energy required for growth (J day^{-1}) can be derived from laboratory or field estimates of growth (g day^{-1}) multiplied by the energy equivalent of shark tissue (J g^{-1}), which to date has only been determined for juvenile lemon sharks (5.41 kJ g^{-1} [wet weight]; Cortés and Gruber, 1994) and scalloped hammerhead pups (6.07 kJ g^{-1} ; Lowe, 2002). The daily energy required for total metabolic expenditures (J day^{-1}) can be obtained from average daily metabolic rate (for example), expressed as $\text{mg O}_2 \text{ kg shark}^{-1} \text{ day}^{-1}$, multiplied by a standard oxycaloric value of $3.25 \text{ cal ml O}_2^{-1}$ (Elliott and Davidson, 1975) or $13.59 \text{ J ml O}_2^{-1}$, and adjusting for shark mass (kg). The energy lost as non-assimilated food (urine and feces) has only been measured in the lemon shark (Wetherbee and Gruber, 1993), where it represented approximately 27% of the total ingested energy. This proportion of energy corresponding to $F + U$ can be substituted into the bioenergetic equation by multiplying $G + M$ by a factor of 1.37 (to account for energy losses). The final step is to use the energy value of food consumed (J g^{-1}), divide it into $1.37(G + M)$, and express the result as a percentage of body weight. Cortés and Gruber (1990) used a variation of this bioenergetic approach to estimate daily ration for juvenile lemon sharks; i.e., they used a laboratory-derived feeding rate–growth rate curve (also known as G – R curve) to estimate daily ration in the wild as the food intake level that corresponded to field-observed growth.

Table 8.1 summarizes studies of food consumption rates in elasmobranchs, including the shape of the model that best described the rate of gastric evacuation, total gastric evacuation time, estimates of daily ration, and gross conversion efficiency. Feeding rates of elasmobranchs — at least on a body weight basis — are considerably lower than those of many teleosts (Brett and Groves, 1979), even with the inclusion of sharks fed to satiation in captivity, and rarely surpass $3\% \text{ BW day}^{-1}$ (Table 8.1). In addition, consumption rates of adults may decrease by an order of magnitude with respect to those of pups, as found for captive sevengill sharks (*Notorynchus cepedianus*) fed to satiation (Van Dykhuizen and Mollet, 1992; Table 8.1) and in bioenergetic estimates for the bonnethead (*Sphyrna tiburo*; E. Cortés, unpubl.).

8.3.2 Gastric Evacuation

Estimation of daily ration through *in situ* methods requires knowledge of gastric evacuation rates. As in many areas of elasmobranch research, our ability to conduct controlled field or laboratory experiments is severely impaired by the difficulty of maintaining large individuals, which has resulted in experiments conducted on small species or juvenile stages of larger species (Cortés, 1997).

Cortés (1997) pointed out that there is still considerable debate about the adequacy of the most common mathematical models (linear, exponential, square root, surface area) used to describe gastric evacuation in fishes, and that no single model can be used to represent the dynamics of different species consuming different prey under different environmental conditions in all cases. The physiological rationale for the various models of gastric evacuation and the statistical adequacy of the criteria used to select the best model of evacuation have been extensively reviewed elsewhere (see references in Cortés, 1997). Cortés (1997) advocated the use of multiple measures of statistical fit along with formal residual analysis and an examination of residual plots before selecting a model, but pointed out that even with thorough analyses results may still be inconclusive. A sensible approach for estimating daily ration through *in situ* methods is therefore to evaluate the effects of various evacuation models.

TABLE 8.1

Summary of Gastric Evacuation, Daily Ration, and Food Conversion Efficiency Estimates for Elasmobranchs

Species	Stage	GE Curve	TGET (h)	Daily Ration (% BW day ⁻¹)	K ₁ (%)	Ref.
<i>Carcharhinus acronotus</i>	Juvenile, adult	—	—	0.87–1.56 ^a (28)	—	Carlson and Parsons (1998)
<i>Carcharhinus dussumieri</i>	Juvenile (10)	—	—	2.91 ^b (26–30)	—	Salini et al. (1999)
<i>Carcharhinus leucas</i>	Pup (6)	—	—	0.50 ^c (24)	—	Schmid et al. (1990)
	Pup (5)	—	—	—	5–12 ^c (23–25)	Schmid and Murru (1994)
<i>Carcharhinus melanopterus</i>	Juvenile (20)	—	—	0.3–0.8 ^c (22–28)	20 ^c (22–28)	Taylor and Wisner (1989)
<i>Carcharhinus plumbeus</i>	Juvenile	Gompertz	81–104 (22–26; 17)	0.9–1.3 ^a (25; 414)	14.1 (25)	Medved (1985), Medved et al. (1988)
	Nr (3)	—	>48 (nr)	—	—	Wass (1973)
	Pup	—	—	1.43 ^a (18.5)	—	Stillwell and Kohler (1993)
	Juvenile, adult	—	—	0.86 ^a (18.5)	—	Stillwell and Kohler (1993)
	Adult (6)	—	—	0.47 ^c (24)	—	Schmid et al. (1990)
<i>Carcharhinus tilstoni</i>	Juvenile (4)	—	—	3.44 ^b (26–30)	—	Salini et al. (1999)
<i>Negaprion acutidens</i>	Juvenile (4)	—	—	3.35 ^b (26–30)	—	Salini et al. (1999)
<i>Negaprion brevirostris</i>	Juvenile	Linear	28–41 (20–29; 48)	1.5–2.1 ^d (23–32; 86)	9.4–13.1 (32) [–64–25] ^f (25; 80)	Cortés and Gruber (1990, 1992, 1994)
	Juvenile	Exponential	24 (25; 20)	—	—	Schurdak and Gruber (1989)
	Juvenile	—	—	2.7 ^b (25; 6)	[22.4] ^e (25; 3)	Gruber (1984); Longval et al. (1982)
	Juvenile (1), adult (1)	—	—	0.5–1.4 ^b (21–29)	—	Clark (1963)
<i>Prionace glauca</i>	Nr	—	>24 (14–16; 3)	—	—	Tricas (1979)
	Adult	Exponential ^f	164 (19; 2)	0.40–0.65 ^d (17; 54)	17.1 (17)	Kohler (1987)
<i>Sphyrna lewini</i>	Juvenile	Multiple ^g	>5–29 (21–29; 64)	2.12–3.54 (22–28; 451)	—	Bush and Holland (2002)
	Juvenile	—	—	—	2.9–9.4 ^a (26)	Lowe (2002)
<i>Sphyrna tiburo</i>	All	Logistic	>50 (20–30; 46)	2.16–4.34 ^d (20–30; 53)	—	Tyminski et al. (1999)
<i>Triakis semifasciata</i>	All	Linear	28–32 (13–18; 30)	0.85–2.20 (nr; 138)	—	Kao (2000)
<i>Schroederichthys chilensis</i>	Nr	Exponential	74 (16; 18)	—	—	Aedo and Arancibia (2001)
<i>Scyliorhinus canicula</i>	All	Surface area ^h	50–>70 (14; 237)	—	—	Macpherson et al. (1989)
	Adult	Exponential	>200 (15; 20)	—	—	Sims et al. (1996)
<i>Isurus oxyrinchus</i>	Adult	—	36–48 ⁱ	2.2–3.0 ^c (19)	—	Stillwell and Kohler (1982)
<i>Carcharias taurus</i>	Adult (13)	—	—	0.27 ^c (24)	—	Schmid et al. (1990)
<i>Ginglymostoma cirratum</i>	Adult (6)	—	—	0.31 ^c (24)	—	Schmid et al. (1990)
<i>Notorynchus cepedianus</i>	Pup	—	—	2 ^c (12–14)	25–40	Van Dykuizen and Mollet (1992)
	Juvenile	—	—	0.6 ^c (12–14)	10–15	
	Adult	—	—	0.2 ^c (12–14)	—	

TABLE 8.1 (Continued)

Summary of Gastric Evacuation, Daily Ration, and Food Conversion Efficiency Estimates for Elasmobranchs

Species	Stage	GE Curve	TGET (h)	Daily Ration (% BW day ⁻¹)	K ₁ (%)	Ref.
<i>Squalus acanthias</i>	Juvenile, adult	—	124 (10; 75)	1.3 ^b (10; 5) 0.4 ^k (10)	6.1–10.7 ^j	Jones and Geen (1977) Holden (1966)
	Adult	—	—	1.5–2.0 ^a (10)	—	Brett and Blackburn (1978)
	Adult	—	>48 (15)	—	—	Van Slyke and White (1911)
	All	—	—	2.60 ^l (nr; 3396)	—	Tanasichuk et al. (1991)
<i>Dasyatis sabina</i>	All	Exponential ^f	—	2.52 (27–33; 48)	—	Bradley (1996)
<i>Gymnura altavela</i>	Adult (2)	—	—	—	10.8 ^e (23)	Henningson (1996)
<i>Raja erinacea</i>	All	Multiple ^g	12–52 ^m (10 and 16; 28)	—	—	Nelson and Ross (1995)
<i>Callorhynchus callorhynchus</i> ^a	All	—	>24 (13, 113)	1.36 (11.5–13, 181)	—	Di Giacomo et al. (1994)

Note: Abbreviations: GE curve is the mathematical model that best describes gastric evacuation; TGET is total gastric evacuation time; K₁ is gross conversion efficiency (annual production divided by annual consumption estimates); Nr is not reported; Single values in parentheses denote temperature range in degrees Celsius, except for the Stage column, where they indicate sample size; a second value indicates sample size.

^a Bioenergetic estimate(s) only.

^b Captive sharks fed experimental meal to satiation.

^c Food consumed by captive sharks in display aquarium.

^d Includes both *in situ* and bioenergetic estimates.

^e Derived in laboratory or aquarium experiments where sharks were fed at varying ration sizes and growth recorded.

^f Assumed functional relationship.

^g Different models provided the best fit depending on temperature, food type, or meal size.

^h Gastric evacuation of small prey items was adequately described by exponential model.

ⁱ Assumed values.

^j 6.1% is for age 1 dogfish, 10.7% is for age 0 dogfish.

^k “Working” bioenergetic estimate.

^l Estimated from mean stomach fullness indices.

^m Depending on temperature and food type.

ⁿ A holoccephalan.

In addition to the well-known accelerating effect of temperature (Brett and Groves, 1979), meal size and food type also seem to affect the gastric evacuation dynamics of elasmobranchs. Larger meal sizes generally take longer to digest and evacuate (Sims et al., 1996; Bush and Holland, 2002). In general, it appears that small, more friable, and easily digestible items are evacuated more quickly than larger items with lower surface-to-volume ratios (Medved, 1985; Schurdak and Gruber, 1989; Cortés and Gruber, 1992; Nelson and Ross, 1995). Surface area models provided the best fit to gastric evacuation data for the lesser spotted dogfish, especially when the meal included more than one prey item (Macpherson et al., 1989). Most species of elasmobranchs consume different types of prey, which in turn may be evacuated from the stomach at different rates, and thus greatly influence estimates of daily ration based on gastric evacuation rate. For example, Medved (1985) found that time required for evacuation of crab and teleost prey from the stomachs of sandbar sharks could differ by as much as 20 h. In general, the effects of food type, number and digestibility of prey, and meal size on gastric evacuation dynamics of elasmobranchs would clearly improve the accuracy of estimates of daily ration and overall rates of consumption.

The sequence of digestion and gastric evacuation of foodstuffs in elasmobranchs has not been fully elucidated. An initial lag phase before the start of gastric evacuation into the intestine, attributed to the time required for gastric juices and enzymatic reactions to take effect, was reported for the sandbar shark (Medved, 1985); however, this delay in the onset of digestion may have resulted from handling and force feeding of experimental animals (Wetherbee et al., 1990). In fishes, initial chemical digestion is generally attributed to pepsin, an acid protease (Holmgren and Nilsson, 1999). Plots of the change in energy content of the ingested meal with time suggested that tissues with higher energy, such as muscle, were evacuated before lower-energy tissues, such as exoskeleton, during the earlier stages of gastric evacuation in gray smoothhound sharks (*Mustelus californicus*; San Filippo, 1995). In contrast, Shurdak and Gruber (1989) reported that carbohydrates were evacuated from stomachs of lemon sharks prior to evacuation of proteins. For a detailed description of the anatomy and physiology of the digestive system of elasmobranchs readers are referred to Holmgren and Nilsson (1999).

Although research for skates and rays is extremely scarce, emptying of food from the stomachs of elasmobranchs takes considerably longer than in teleosts. With very few exceptions, it takes a minimum of one to — often — several days to completely evacuate a meal from the stomach of elasmobranchs (Table 8.1). Presumably, lamnid sharks, such as the white shark, and other species capable of elevating stomach temperature above ambient water temperature through countercurrent mechanisms (McCosker, 1987; see Carlson et al., Section 7.5 of this volume) could have rapid rates of digestion, but no gastric evacuation measurements have been made to date on such heterothermic species.

8.4 Excretion and Egestion

A portion of food that is consumed by elasmobranchs is not absorbed by the digestive tract and is egested as feces. Additionally, a portion of the food that is absorbed by intestinal cells is not available for the energetic demands of the animal and is excreted as nitrogenous waste in urine and gill effluent.

8.4.1 Excretion

Energetic losses in gill effluent and urine have not been measured in elasmobranchs, but have been presumed to be similar in scale to losses (about 7% of the energy budget) estimated for teleost fishes (Brett and Groves, 1979). Quantification of energy losses through the gills and kidneys of elasmobranchs is problematic due to the large quantity of water involved in housing elasmobranchs, as well as retention of nitrogenous wastes in the form of urea and trimethylamine oxide in blood and tissues for osmoregulatory purposes (Perlman and Goldstein, 1988; Wood, 1993; Evans et al., Chapter 9 of this volume).

8.4.2 Egestion

Elasmobranchs have a spiral valve intestine, which functions to increase surface area for digestion and absorption of food, but which also conserves space in the body cavity for a large liver and development

of large embryos (Moss, 1984). The digestive capability of the spiral valve intestine has been investigated in only one species of elasmobranch, the lemon shark (Wetherbee and Gruber, 1993). These authors used an indirect method of measurement incorporating an inert, naturally occurring marker (acid-insoluble ash) into food. In this study, lemon sharks were capable of absorbing energy and nutrients in food with an average efficiency close to 80%, which is similar to many carnivorous teleosts. However, the time required for a meal to be completely eliminated from the digestive tract of lemon sharks was prolonged (70 to 100 h) in comparison to most teleosts (Wetherbee et al., 1987; Wetherbee and Gruber, 1990). Other studies have reported that food remains in the digestive tract of elasmobranchs for long periods of time (up to 18 days) in comparison to most teleosts (Wetherbee et al., 1990; Sims et al., 1996). The protracted periods of time required for complete food passage, in addition to difficulties involved with maintaining sharks in captivity and the labor-intensive methods required for fecal collection, present major obstacles for studies on digestive efficiency of sharks (Wetherbee and Gruber, 1993).

Prolonged passage of food through digestive tracts of elasmobranchs may be required for spiral valve intestines to accomplish digestion and absorption of food at levels comparable with those of teleosts. There have been several studies on enzymatic digestion in the stomachs of elasmobranchs, but few studies on pancreatic and brush border enzymes that function to break down macromolecules to smaller subunits for absorption across the intestinal epithelium (Sullivan, 1907; Van Slyke and White, 1911; Fänge and Grove, 1979; Caira and Jolitz, 1989; Papastamatiou, 2003). Although the relationship between prolonged food passage time and limitation of enzymatic digestion in elasmobranchs is unknown, it is apparent that prolonged food passage is related to a low rate of consumption in sharks, which in turn limits growth and reproductive rates. Although low rates of food consumption may provide evolutionary advantages for elasmobranch populations, the associated low growth and reproductive rates are life history characteristics that contribute to the vulnerability of the majority of elasmobranch populations to overfishing.

8.5 Production

Production, or growth in body mass, can be measured through laboratory experiments, field mark-recapture methods, or indirectly through size at age relationships. Relative rates of production (expressed as percent body weight) of most teleost species are considerably higher than those of elasmobranchs (Wetherbee et al., 1990), with many teleosts doubling their body weight in less than a week after birth (Brett and Groves, 1979). Relative growth rates in length and mass are much higher for immature than mature individuals in most elasmobranch species (see Cailliet and Goldman, Chapter 14 of this volume), especially during the first year of life. Branstetter (1990) estimated first-year growth in body length for several shark species, with values ranging from 16 to 100% per year. Wetherbee et al., (1990) reported values of first-year growth in mass of 33, 79, and 138% for the spiny dogfish, sandbar shark, and lemon shark, respectively. In relative terms, small coastal and pelagic species tend to grow at a faster rate than their large coastal counterparts, probably reflecting differences in the risk of predation faced by juveniles. As very few estimates of food consumption are available, it is unclear whether differences in production are a result of different food consumption or different energy allocation.

Growth efficiency measures have very seldom been calculated in elasmobranchs. The efficiency of food conversion to somatic growth, or gross conversion efficiency (K_1), is important ecologically because it measures the proportion of ingested food that will be available to the next trophic level (Warren and Davis, 1969). K_1 values reported for elasmobranchs range from about 3 to 40% (Table 8.1). Van Dykhuizen and Mollet (1992) reported that K_1 values (which they referred to as cumulative total efficiency) decreased with increasing age, from 25 to 40% at age 1 to 3 years to 10 to 15% at age 5 to 6 years in aquarium-fed sevengill sharks. Most K_1 values for elasmobranchs (Table 8.1) are comparable to values reported for teleosts (10 to 25%; Brett and Groves, 1979), indicating that elasmobranchs are generally capable of converting energy to growth as efficiently as teleosts.

The rate of production and K_1 are functions of the rate of food consumption. Only one study has examined this relationship in elasmobranchs. Cortés and Gruber (1994) found that the relationship

between production rate and feeding rate in juvenile lemon sharks was best described by a von Bertalanffy growth-like equation of the form:

$$G_r = G_{\max}(1 - e^{-k(R-R_m)}) \quad (8.3)$$

where G_r is growth rate, G_{\max} is maximum growth rate, k is the rate of change in growth rate with feeding rate, R is feeding rate, and R_m is the maintenance ration (no growth). They reported very similar values of $R_m = 1.06\%$ wet BW day⁻¹ and G_s (loss in weight due to starvation) = 1.11% BW day⁻¹. Cortés (1991) also estimated a value for R_{opt} , the optimal ration (Pandian, 1982), of 2.15 BW day⁻¹ for a 2-kg lemon shark in its first year of life, by drawing a tangent from the origin of coordinates in the G - R curve to the point in the curve with the steepest slope. Cortés and Gruber (1994) found values of K_1 ranging from -64% to 25%, and that K_1 slowed, but continued to increase, at ration levels above maintenance. This finding did not support those from several studies with teleosts where a dome-shaped curve was found (Paloheimo and Dickie, 1966), and K_1 rapidly decreased after reaching a peak at an optimum feeding rate. The efficiency of conversion of absorbed food to growth, or net conversion efficiency (K_2), has not been measured for any elasmobranchs, except for an estimate of 33% provided by Gruber (1984) for juvenile lemon sharks.

8.6 Conclusions

The major prey item consumed by elasmobranchs is teleost fishes; however, there are numerous exceptions to this generalization. Accurate descriptions of the diets of elasmobranchs are complicated by the plasticity of their feeding habits, which regularly result in ontogenetic and spatiotemporal shifts. Based on determinations for a limited number of species, sharks appear to exhibit short feeding bouts followed by longer periods of digestion. The food consumption dynamics of elasmobranchs may ultimately be governed by a morphological peculiarity of this group of predators, a spiral valve intestine. This digestive morphology likely dictates slower rates of gastrointestinal emptying, lower food consumption rates, lower production rates, and generally slower food dynamics for elasmobranchs compared to teleosts. From our limited knowledge, however, it appears that elasmobranchs are capable of absorbing food and converting it to growth with efficiencies comparable to those of teleosts.

Another peculiarity, the physiological adaptation of elasmobranchs for retention of high levels of urea in their blood and tissues, may complicate estimation of trophic levels through stable isotope analysis and quantification of energy losses in gill effluent and urine for bioenergetic studies. Clearly, much remains to be learned about food consumption and feeding habits of elasmobranchs. Because of the difficulty of conducting controlled experiments with large, adult individuals of many elasmobranch species, we advocate a pragmatic approach to advance our knowledge of the feeding ecology of this group.

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